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INFANTICIDE VERSUS ADOPTION: AN INTERGENERATIONAL CONFLICT

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Abstract.—Considerable attention has been paid to the phenomenon of infanticide in recent years. Five functional categories of infanticide have been defined. Here I concentrate on those that either have been described as the outcome of possible competition for limited resources or have by default been classified as the result of social pathology. Many of the species that show infanticide of this nature also show adoption of unrelated young at fairly high frequencies. I suggest that the possibility of caring for nonfilial offspring creates an intergenerational conflict, or arms race, whereby offspring separated from their parents or receiving parental care of substandard quality (insufficient for their survival) should be selected to solicit care from adults other than their parents and the potential adoptive parents are selected to avoid giving such care. Evidence suggests that most examples of supposedly pathological infanticide, or resource-based infanticide, are the result of potential foster parents killing unrelated offspring when these offspring can clearly be identified as nonrelatives. Support for this idea comes from observations that (1) such infanticide is most common in group-living or colonial species, where chances of encountering wandering offspring are high; (2) infanticidal individuals come almost exclusively from the sex that bears the primary costs of adoption; (3) such infanticide occurs only under conditions where victims can clearly be identified as nonfilial; and (4) in species with little or no cost to adoption, adoption is common, but infanticide is nonexistent.

In recent years, a great deal of attention has been paid to the phenomenon of infanticide (reviews in Hausfater and Hrdy 1984). Five major functional categories of infanticide have been defined: (1) exploitation of the infant as a food resource, that is, cannibalism; (2) sexual selection: individuals (typically males) improve their opportunities for breeding by eliminating dependent offspring of a prospective mate; (3) parental manipulation: parents increase their own reproductive success (on average) by eliminating particular offspring; (4) competition for resources: death of the infant potentially increases resource availability either for the killer or its descendants; and (5) social pathology: killing of unrelated offspring with no adaptive explanation (from Hrdy 1979; Hrdy and Hausfater 1984).

Numerous cases of infanticide involve breeding adults that attack and kill offspring of other breeding adults (e.g., Davis and Dunn 1976; Pierotti 1980, 1982*a*, 1988; Hausfater and Hrdy 1984 and reviews therein; Hoogland 1985; Pierotti and Murphy 1987). In many of these cases, offspring are not eaten, which eliminates cannibalism (category 1) as an explanation. Category 2 (sexual selection) can be eliminated in many other cases since the killer does not kill offspring of prospec-

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tive mates. Category 3 (parental manipulation) can be eliminated since the killer is not killing its own offspring.

Elimination of categories 1–3 in these cases leaves only categories 4 and 5 as possible explanations. Category 4, competition for resources (Pierotti 1980, 1982*a*; Sherman 1981), is easily invoked, but this is the most difficult category to demonstrate convincingly (Hrdy and Hausfater 1984). As a consequence, competition for resources and social pathology have become default explanations for many cases of infanticide.

This reliance on alleged resource competition and social pathology is unsatisfying. Resource competition is a nebulous concept and could be invoked in any situation since it can be argued that killing a conspecific will always reduce potential competition for resources. To satisfactorily demonstrate that infanticide occurred to reduce competition, it must be shown that (*a*) the resource in question is actually limiting and (*b*) killers, or their relatives, thereby gain increased access to that resource. Similarly, pathology can always be invoked when one conspecific kills another. For pathology to be established, it must be convincingly argued that the infanticidal individual is behaving in a manner that indicates malfunction.

In this article, I examine the evidence in relation to an alternative explanation for cases of infanticide that have been attributed to either competition for resources or social pathology, that is, avoidance of adoption and provision of parental care to unrelated offspring (Pierotti and Murphy 1987; Pierotti 1988; see also Sherman 1981; Elwood and Ostermeyer 1984; Mock 1984). I do not discuss cases of infanticide that have solid functional explanations. These include instances where the infanticidal adult kills its own offspring to increase chances of survival of itself or of other offspring (parental manipulation) or kills offspring of prospective mates in order to bring the mates into sexually receptive condition, for example, male langurs or lions. In cases where the infanticidal adult consumes or partially eats the offspring it kills, the exact cause of the infanticide may be problematical. As a result, I discuss below several cases where cannibalism occurs in conjunction with infanticide.

THE INTERGENERATIONAL CONFLICT HYPOTHESIS

All of the proposed explanations of infanticidal behavior ignore the possible role of the offspring in the interaction and treat offspring as if they were passive recipients of their fate. This may be an important oversight, for there will always be strong selection on traits that maximize chances of offspring survival to independence regardless of parental interests (Trivers 1974; Pierotti and Murphy 1987; Pierotti 1988). In most natural populations, some offspring receive inadequate parental care because they have become separated from their parent(s), a parent has died, or their parents are inexperienced or inept. Under these circumstances, selection would exist for traits that enable young to solicit parental care from adult individuals other than their biological parents (Mock 1984; Pierotti and Murphy 1987; Pierotti 1988).

Adoption or care of unrelated offspring has been reported from a number of species in which infanticide that has been attributed to either competition for resources or social pathology has also been reported (tables 1 and 2). The re-

TABLE 1

SPECIES OF MAMMALS FROM WHICH BOTH ADOPTION AND INFANTICIDE ATTRIBUTED TO COMPETITION FOR RESOURCES OR SOCIAL PATHOLOGY HAVE BEEN DESCRIBED, AND THE CHARACTERISTICS OF THESE SPECIES THAT RELATE TO PREDICTIONS RELATED TO INTERGENERATIONAL CONFLICTS

Species	Group Living	Sex Making Primary Parental Investment	Infanticidal Sex	Reference(s)
Human (*Homo sapiens*)	Yes	Male/female	Male/female	Daly and Wilson 1984, 1988
Wild dog (*Lycaon pictus*)	Yes	Female	Female	Van Lawick 1973
Dingo (*Canis dingo*)	Yes	Female	Female	MacDonald and Moehlman 1984
Wolf (*C. lupus*)	Yes	Female	Female*	McLeod 1990
Domestic cat (*Felis domesticus*)	Yes	Female	Female*	Turner and Bateson 1988
Lion (*Panthera leo*)	Yes	Female	Female*	Bertram 1975
Northern elephant seal (*Mirounga angustirostris*)	Yes	Female	Female*	Riedman and LeBoeuf 1983
Southern elephant seal (*M. leonina*)	Yes	Female	Female*	Riedman 1990
Hawaiian monk seal (*Monachus schauinslandi*)	Yes	Female	Female	Boness 1990
Grey seal (*Halichoerus grypus*)	Yes	Female	Female	Fogden 1971
Weddell seal (*Leptonychotes weddelli*)	Yes	Female	Female	Riedman 1990
Walrus (*Odobenus rosmarus*)	Yes	Female	Female	Riedman 1990
Antarctic fur seal (*Arctocephalus gazella*)	Yes	Female	Female	Riedman 1990
Australian sea lion (*Neophoca cinerea*)	Yes	Female	Female	Riedman 1990
Steller sea lion (*Eumetopias jubatus*)	Yes	Female	Female*	Riedman 1990; R. Pierotti, personal observation
Belding's ground squirrel (*Spermophilus beldingi*)	Yes	Female	Female*	Sherman 1981
Columbian Ground squirrel (*S. columbianus*)	Yes	Female	Female	Balfour 1983; Waterman 1984
Black-tailed prairie dog (*Cynomys ludovicianus*)	Yes	Female	Female*	Hoogland 1985
Deer mouse (*Peromyscus* spp.)	No	Female	Female	Hansen 1957
House mouse (*Mus musculus*)	Yes	Female	Female*	Brown 1953
Black rat (*Rattus rattus*)	Yes	Female	Female*	Rosenblatt 1990
Woodrat (*Neotoma* spp.)	No	Female	Female	Egoscue 1957; Fleming 1979
Muskrat (*Odonatra zibetica*)	No	Female	Female	Errington 1963
Lemming (*Lemmus* spp.)	Yes	Female	Female	Arvola et al. 1962
Lemming (*Dicrosonyx* spp.)	Yes	Female	Female*	Boonstra 1980
Steppe lemming (*Lagurus lagurus*)	Yes	Female	Female	Nowak and Paradiso 1983
Vole (*Microtus* spp.)	Yes	Female	Female*	Brooks 1984
Wild boar (*Sus scrofa*)	Yes	Female	Female	Riedman 1982
Domestic goat (*Capra hircus*)	Yes	Female	Female	Riedman 1982

* Either cannibalistic or sexually selected infanticide also reported from this species under certain circumstances.

TABLE 2

COMPARISON OF OVERALL PATTERN OF GROUP-LIVING AND NON-GROUP-LIVING MAMMALS AND BIRDS AGAINST PATTERN OF SPECIES SHOWING BOTH ADOPTION AND INFANTICIDAL AGGRESSION

	Species Exhibiting Adoption/Infanticide	All Species Combined
A. Mammals:		
Group-living	27*	1,590†
Non-group-living	3	2,530
B. Birds:		
Group-living	25‡	2,600§
Non-group-living	5	6,300

* $\chi^2 = 24.81$, $P < .001$, df = 1.
† Data from Nowak and Paradiso (1983) and Wilson (1975).
‡ $\chi^2 = 39.98$, $P < .001$, df = 1.
§ Data from Lack 1968.

peated co-occurrence of adoption and infanticide suggests an alternative interpretation. Charlesworth (1980) has argued that traits may appear that affect different stages of the life cycle. It is possible that a trait could evolve that acts on offspring receiving inadequate parental care to solicit care from unrelated adults (see above). Traits could also evolve, however, for adults to avoid caring for unrelated offspring whenever there exists a potential cost in fitness to such behavior (Riedman 1982). These counteracting traits (or forces of selection favoring these traits) set up an intergenerational conflict in which offspring are attempting to elicit care from adults that are selected to avoid providing such care.

In species where there is a high probability either of adults providing inadequate care or of offspring becoming separated from their parent(s), adults may attack and kill any offspring that can be unambiguously identified as not their own (see also Sherman 1981; Mock 1984). In mammals and species of birds with altricial young, infanticidal attacks should be directed at eggs or newborn offspring of neighbors still in the natal nest, where they can be unambiguously identified as nonfilial. If these individuals survive to move around, they may enter broods other than their natal broods, where adults will be unable to distinguish them at this time without risking injury to filial offspring. Such a wandering offspring could succeed in establishing itself with an unrelated adult, for example, by mixing in with the filial offspring and being adopted and reared, possibly at some fitness cost to the adult (Riedman 1982).

In general, this conflict will be dynamic, with selective pressure on adults to discriminate being greater when their own fitness costs are higher, that is, when the survival of the adult's own offspring, or even the survival of the adult itself, will be reduced by caring for a nonrelative. Despite these costs, however, juveniles might be expected to win most such conflicts for two reasons: first, there is a cost asymmetry in that strength of selection on the offspring will often exceed the strength of selection on the adults since an offspring that fails to receive adequate care will die, while the adult that provides the care generally loses only

time and energy and, perhaps, some residual reproductive value, and, second, if two traits have similar effects on fitness and at least one trait acts within the reproductive period, selection will act most strongly on the trait that is expressed earlier in the life cycle (Charlesworth 1980, p. 208).

Several predictions can be generated about this conflict and the occurrence of adoption and infanticidal behavior. First, infanticide to prevent provision of care to unrelated offspring should occur primarily in species where chances of encountering wandering offspring that might solicit care are high, for example, in group-living birds and mammals where individuals live in close proximity to one another when rearing young. Second, the individuals that commit such infanticide should be those individuals that sustain the greatest cost from adoption, that is, female mammals that would sustain a high cost of lactation, or males of monogamous or polyandrous species of birds where costs of chick rearing are much higher in males than in females. Third, adoption in combination with infanticide should occur most frequently in species that have multiple offspring per brood or litter, where the chances of mixing in with a number of individuals are higher. Finally, adoption should be relatively common, and infanticide rare or nonexistent, in species where there are no costs and some potential benefits to adoption, for example, in birds with precocial offspring, or fishes, where the only care provided is guarding the brood from predators and the costs of such care are not increased by additional offspring. In such cases there may actually be a benefit from adoption since increasing flock or litter size may dilute the impact of predation through a selfish herd effect (Hamilton 1971).

Of these four predictions, only group living (1) does not allow a clear distinction between resource competition and avoidance of adoption since it could be argued that group living could contribute to increased competition for resources as well as increased chances of adoption. Infanticide by the sex bearing the primary cost of adoption (2), and the absence of such infanticide in species where costs of adoption are negligible (4), is clearly related to costs of adoption and their avoidance. If competition for resources were the cause, infanticide should be committed without regard to costs of caring for unrelated offspring and would always be favored. Similarly, if resource competition is important, deadly aggression should be directed at weaned or fledged individuals that represent serious competition for both adults and their own recently independent offspring, rather than at neonates or nestlings.

Finally, it should be emphasized that under certain circumstances, it will be difficult to distinguish between resource-based and adoption-avoidance infanticide, especially in long-lived species where adoption of additional young could be a nutritional drain on parents but young also benefit from local resources beyond direct care during the period of dependency.

MAMMALS

Mammals that have exhibited infanticidal behavior characterized as pathological or as the result of resource competition include pinnipeds (Fogden 1971; LeBoeuf and Briggs 1977; Boness 1990; Riedman 1990), carnivores (MacDonald

and Moehlman 1984), a variety of rodents (Labov 1980; Mallory and Brooks 1980; Sherman 1981; Michener 1982; Balfour 1983; Brooks 1984; Elwood and Ostermeyer 1984; vom Saal 1984; Waterman 1984; Hoogland 1985; Grossman 1987), a few ungulates (Riedman 1982; Teillaud and Campan 1987), and *Homo sapiens* (Daly and Wilson 1984, 1988).

In accordance with prediction 1, of the 30 species that show both adoption and unexpected infanticide, 27 are group-living (tables 1 and 2). Compared with the overall percentage of group-living (39%) to non-group-living mammals (61%), the difference is highly significant. ($P < .001$ by χ^2 test; table 2, pt. A: the results in table 2, pt. A are based on my counts of data from Nowak and Paradiso [1983] and Wilson [1975]. Eisenberg [1981] reporting data on sociality from 59 "representative" species of mammals shows 25 [42%] to be group-living [tables 58 and 59, pp. 423–425]. The difference between my results and those of Eisenberg is not significant by χ^2 test. Regardless of whether we use my results [table 2, pt. A], those of Eisenberg, or split the difference and argue that 40% of mammalian species are group-living, the difference between these results and the percentage of group-living species that show adoption and infanticide are highly significant by χ^2 test.)

Prairie dogs (*Cynomys* spp.) live in large colonies containing hundreds of individuals (Hoogland 1985; Grossman 1987). Ground squirrels (*Spermophilus* spp.), voles and lemmings (*Microtus* spp. and *Dicrostonyx* spp.), and deer mice (*Peromyscus* spp.) live in smaller aggregations of 10–25 individuals (Sherman 1981; Brooks 1984). Young rodents of these species may seek care by females other than their mothers after emerging from the natal den (Sherman 1981; Hoogland 1985). Pinnipeds from which adoption and aggression directed at newborns have been reported breed primarily in aggregations consisting of hundreds or thousands of individuals (Bartholomew 1970; Riedman 1990). Young pinnipeds have a high probability both of becoming separated from their mothers and of encountering potential adoptive parents if they do become separated.

In 20 of 21 species of mammal that showed presumed pathological or resource-based infanticide, females were the primary infanticidal sex (table 1; but see below). In all of these species, the female performs most or all of parental care. The only exceptions are male canids that provide food for females and offspring (MacDonald and Moehlman 1984) and male rodents of some species that attend, guard, and groom offspring (Brooks 1984; Grossman 1987). Energetically, the most costly phase of parental care in mammals is lactation (Hayssen 1984; Oftedahl 1985). Therefore, nearly all of the physiological cost (and potential fitness costs) are borne by females.

Males of several of these species were also observed to be infanticidal, but all of these cases involved either cannibalism, sexual selection, or both (table 1). The one possible exception is *Homo sapiens,* where male investment in offspring can be high (Daly and Wilson 1988). If we assume that unexplained cases of infanticide should be equally likely to be committed by males and females, the tendency for female mammals to be the infanticidal sex is highly significant ($P < .001$ by χ^2 test).

In accordance with prediction 3, in 19 of the 21 species, females produce multi-

ple offspring per litter. Of the two remaining species, elephant seals, *Mirounga angustirostris,* breed in very dense aggregations where the chances of confusion of offspring are high. The other species is *Homo sapiens*.

Case Studies

In northern elephant seals and Hawaiian monk seals, the major cause of mortality in newborn pups is attacks by reproductive females (LeBoeuf and Briggs 1977; Boness 1990). Most attacks involve bites to the head and the tossing away of pups that approach females with pups. Such bites and tossing result in severe injuries including crushed skulls, severe hematomas, and broken postcranial bones (LeBoeuf and Briggs 1977; R. Pierotti, personal observation). Some pups are also crushed by adult males during rushes through the breeding aggregation, but this mortality is an incidental result of male-male competition and not the result of attacks directed specifically at pups.

Monk seals and elephant seals also show high rates of adoption (Riedman and LeBoeuf 1983; Boness 1990). During disturbances on the elephant seal colonies, that is, male fights or storms during which breeding beaches become awash, many pups become separated from their mothers. These pups seek care from any female that will accept them, and in a given year a substantial proportion (from 5% –10% to over 90%) of female elephant seals are raising an unrelated offspring, including females raising more than one pup (Riedman and LeBoeuf 1983; R. Condit, personal communication). Therefore, during a typical reproductive life span (7–10 yr; Riedman and LeBoeuf 1983), the chances are very high that a female will raise one or more unrelated offspring. Females could prevent this by attacking, and sometimes killing, any pup that approaches them when they already have a pup with them.

In black-tailed prairie dogs, as in elephant seals, the major source of juvenile mortality is infanticide (Hoogland 1985; Grossman 1987). Lactating females enter the burrow systems of other females and kill more than 30% of all litters, including those born to close kin. After emergence of young from burrow systems, however, female prairie dogs will often suckle unrelated offspring without apparent discrimination (J. Hoogland, personal communication). This suggests that lactating female prairie dogs, as in other mammals (see below), kill offspring that might solicit milk in the future at a time when these offspring can clearly be distinguished from her own offspring, that is, while they are still in the natal den of another female.

Infanticide is also the major cause of death in Belding's ground squirrels (*Spermophilus beldingi*) prior to weaning (Sherman 1981). Most attacks on infants were perpetrated by females, although a substantial number were perpetrated by 1-yr-old males. A major difference between these two categories of killer was, however, that 1-yr-old males killed only a single juvenile and then invariably ate their victims. In contrast, after killing one juvenile, adult females returned to kill others and did not eat their victims. One female was observed to kill four juveniles (Sherman 1981).

Noncannibalistic infanticide has also been observed in Columbian ground squir-

rels (*Spermophilus columbianus*). Most of the perpetrators were lactating adult females, as in Belding's ground squirrels and prairie dogs (Michener 1982; Balfour 1983; Waterman 1984). Although some cannibalism has been observed in this species (F. S. Dobson, personal communication), most infants killed by females were not eaten. In the best-documented case, Balfour (1983) observed a marked lactating female to enter the burrow of a neighbor female on four occasions over a 3-min period, each time emerging with a pup that she killed but did not eat. In Columbian ground squirrels the characteristic increase in aggression between females during lactation has been interpreted as protection of the young from conspecifics (Festa-Bianchet and Boag 1982).

Sherman (1981) argued that infanticide by adult female ground squirrels is an example of competition for a limited resource, in this case safe nesting burrows. Two factors, however, suggest that prevention of adoption might be a good alternative explanation. First, females do not direct their infanticidal attacks solely at female offspring, which would be the actual competitors for nesting burrows, since males disperse out of the natal area (Sherman 1981). Second, infanticidal attacks by females occur only when the young are still in burrows. Sherman (1981) specifically reported that infanticide ceased when pups became ambulatory, that is, capable of moving between dens, yet this is the period when one would expect potential competition for resources to increase markedly. Juvenile ground squirrels have been observed to solicit suckling from females other than their mothers and to join other litters (Sherman 1981). Therefore, the observation that female *Spermophilus* confine their killing of infants to the period when the infants are in the natal den suggests that female ground squirrels, like prairie dogs (see above), may be eliminating potential parasites on their maternal care when they are still in the natal nest and can be unambiguously identified as nonfilial offspring.

In other species of rodents that show infanticide, females are the infanticidal sex (Brooks 1984; Huck 1984). In lemmings, density of adult males has no apparent effect on juvenile survival, but an increase in density of adult females leads to an increase in juvenile mortality (Boonstra 1980). Female Norwegian lemmings kill, but do not eat, intruding juveniles that enter their dens (Arvola et al. 1962). The primary source of nestling and juvenile mortality in wood rats (*Neotoma* spp.) and deer mice (*Peromyscus* spp.) is infanticidal attacks by breeding females (Kinsey 1977; Fleming 1979; Ayer and Whitsett 1980).

Several of these species of rodents show varying degrees of cannibalism of dead offspring, including natal offspring. For example, female house mice will kill and eat their own offspring at high population densities (Brown 1953). Virgin female rats eat neonates that still have birth fluids on their bodies. While licking fluids from the young, they progress directly from licking to eating (Rosenblatt 1990). In prairie dogs, females will partially consume carcasses. In these cases, cannibalism for sustenance may be a contributing factor leading to infanticide. Females may kill to prevent adoption and then consume the carcass as a secondary response. Since adoption has also been reported to occur in many of these species of rodents showing infanticide by females, including wood rats (Egoscue 1957; Fleming 1979), deer mice (Hansen 1957; Ayer and Whitsett 1980), and

lemmings (Arvola et al. 1972; Boonstra 1980), the possibility exists that most or all of this infanticide is directed at young that might seek care from their killers after emerging from the natal nest.

Among carnivores, adoption and infanticide by parental individuals have been reported from several species. Among canids, infanticide by breeding females has been observed in three of the most social species: wolves (*Canis lupus*), dingos (*Canis dingo*), and African wild dogs (*Lycaon pictus;* MacDonald and Moehlman 1984). In felids, the only two group-living species, domestic cats (*Felis domesticus*) and lions (*Panthera leo*), also show female infanticide, although both species also show sexually selected infanticide by males (Bertram 1975).

In group-living canids, only a single female in a pack typically breeds (MacDonald and Moehlman 1984). Offspring produced by subordinate females are generally killed by the dominant breeding female (Van Lawick 1973; MacDonald and Moehlman 1984). In wolves, the dominant female has been observed to enter the den of a breeding subordinate, lick and nuzzle the pups in a manner reminiscent of a mother greeting her offspring, and then kill each pup by biting it (McLeod 1990). This apparent conflict between maternal behavior and the elimination of potential adoptees would be expected in maternal individuals that might potentially care for the offspring if they did not kill them. It is worth noting that, after their pups or kittens have been killed, subordinate females have been observed to suckle the offspring of the dominant female in wolves, dingos, African wild dogs, lions, and domestic cats (MacDonald and Moehlman 1984; H. Feldman, personal communication). Since pack members also provide food for whatever pups are present, the infanticidal female not only reduces her own chances of caring for offspring other than her own but also increases the parental care provided to her own offspring. As in some rodents, female carnivores may eat dead offspring, either their own (McLeod 1990) or those they kill.

The only recorded instances of infanticide by females in ungulates are pigs (*Sus scrofa*) and goats (*Capra hircus;* Polis et al. 1984). Pigs are unusual for ungulates in that they have the most altricial offspring of any ungulate, and parental investment is skewed toward lactation rather than gestation, which would increase the potential costs of adoption. In goats, older females sometimes kill the offspring of younger females. Adoption has been observed to occur in both domestic and wild pigs and in goats under seminatural and wild conditions (Riedman 1982; Teillaud and Campan 1987).

Finally, in *Homo sapiens,* children up to the age of five are seven times more likely to be abused, and many times more likely to be killed, by a stepparent than by a genetic parent (Daly and Wilson 1984, 1988). Abusive stepparents are discriminating and spare their own genetic offspring within the same household (Daly and Wilson 1984, 1988). In a few societies, men acquiring wives with children demand that these children be put to death (Daly and Wilson 1984).

This pattern is observed in both industrialized and nonindustrialized nations, and legends or stories about "cruel stepparents" are reported from a wide range of cultures (Cox 1892; Daly and Wilson 1988). These results should be interpreted cautiously since human behavior may have multiple causes. One possible interpretation, however, is that some humans, while desiring a bond with a particular

mate, may try to avoid making an expensive long-term investment in unrelated offspring. The concentration of stepparent infanticide toward young (>5 yr old) offspring supports this idea. In conjunction with the number of mammalian species that show killing of offspring by potential adoptive parents, the pattern of infanticide by human stepparents shows numerous functional similarities.

BIRDS

Avian examples of alleged pathological or resource-based infanticide have been observed commonly in a number of colonial species with semiprecocial offspring, for example, gulls, terns, skimmers, and murres (Hunt and Hunt 1976; Pierotti 1980, 1982*a;* Mock 1984; table 3). Attacks on fledged offspring soliciting additional care have also been reported from both colonial and more solitary species (Shelley 1934; Brown and Bitterbaum 1980; Leffelaar and Robertson 1985; Bustamante and Hiraldo, in press; Donazar and Ceballos, in press; table 3). Finally, a number of avian species that show cooperative breeding have been observed to remove or "toss," but not eat, eggs, when the eggs are clearly not their offspring (Stanback and Koenig, in press). Such egg tossing is clearly a form of infanticide.

Birds with semiprecocial offspring typically produce small clutches, that is, one to three eggs (Lack 1968). As a result, egg production is not very costly energetically in these species (King 1973; Ricklefs 1974). Incubation is shared by both parents, typically lasts less than a month (Drent 1970; Pierotti 1981, 1987), and does not appear to adversely affect parental condition.

Therefore, the heaviest period of energetic investment in semiprecocial chicks is almost certainly the provision of food and protection for offspring between hatching and fledging. In addition to their own nutritional requirements, parents must meet all of their offsprings' nutritional requirements. Costs involve raising as many as three offspring to adult size within a 4–7-wk period. For adult gulls, genus *Larus,* chick provisioning involves each adult bringing in 40%–50% of its body mass in food per day (Pierotti 1981, 1987). Males of these species bring in larger prey and show significantly higher rates of chick feeding and aggression in defense of young than do females (Montevecchi and Porter 1980; Burger 1981*a;* Pierotti 1981, 1987).

If a breeding pair of birds with semiprecocial offspring adopt any additional offspring, physiological costs increase considerably, especially for males. Rate of feeding gull chicks increases with brood size. In the western gull, *Larus occidentalis,* the highest rate of chick feeding observed was by a male bird that was rearing two unrelated chicks in addition to his own (Pierotti 1982*a*). The mate of this bird did not increase her rate of chick feeding over the mean for the colony, but the male provided food for these offspring at more than twice the mean rate for males, feeding these four chicks an average of 10 times a day. At approximately 100 g/meal, this male gull brought in the equivalent of his body mass in food daily.

As in the mammal species listed above, one of the chief causes of juvenile mortality in birds with semiprecocial offspring is infanticide by breeding adults (Hunt and Hunt 1976; Pierotti 1982*b,* 1987; Fetterolf 1983; Pierotti and Murphy

TABLE 3

SPECIES OF BIRDS FROM WHICH BOTH ADOPTION AND INFANTICIDE ATTRIBUTED TO EITHER RESOURCE COMPETITION OR SOCIAL PATHOLOGY HAVE BEEN DESCRIBED, AND THE CHARACTERISTICS OF THESE SPECIES THAT RELATE TO FOUR PREDICTIONS

Species	Group Living	Sex Making Primary Parental Investment	Infanticidal Sex	Reference(s)
Blue-footed booby (*Sula nebouxi*)	Colonial	Male	Unknown	H. Drummond, personal communication
Egyptian vulture (*Neophron percnopterus*)	No	Unknown	Unknown	Donazar and Ceballos, in press
Osprey (*Pandion haliaetus*)	Yes*	Male	Unknown	Poole 1982
Black kite (*Milvus migrans*)	Yes	Unknown	Unknown	Bustamente and Hiraldo, in press
Red kite (*M. milvus*)	No	Unknown	Unknown	Bustamente and Hiraldo, in press
Imperial eagle (*Aquila heliaca*)	No	Unknown	Unknown	Gonzalez et al. 1986
Prairie falcon (*Falco mexicanus*)	No	Unknown	Unknown	Ellis and Groat 1982
South polar skua (*Catharacta lonnbergi*)	Yes	Male	Male	Mock 1984
McCormick's skua (*C. mccormicki*)	Yes	Male	Male	Mock 1984
Western gull (*Larus occidentalis*)	Colonial	Male	Male	Pierotti 1980, 1981
Herring gull (*L. argentatus*)	Colonial	Male	Male	Pierotti 1980, 1987
Glaucous-winged gull (*L. glaucescens*)	Colonial	Male	Male	Hunt and Hunt 1976
Lesser black-backed gull (*L. fuscus*)	Colonial	Male	Male	Davis and Dunn 1976
Ring-billed gull (*L. delawarensis*)	Colonial	Male	Male	Fetterolf 1983
Common tern (*Sterna hirundo*)	Colonial	Male	Unknown	I. C. T. Nisbet, personal communication
Black skimmer (*Rhynchops nigra*)	Colonial	Male	Male	Burger 1981*b*; J. Quinn, personal communication
Black-legged kittiwake (*Rissa tridactyla*)	Colonial	Male	Male	Pierotti and Murphy 1987
Common murre (*Uria aalge*)	Colonial	Male	Male	Birkhead and Nettleship 1987
Thick-billed murre (*U. lomvia*)	Colonial	Male	Male	Birkhead and Nettleship 1987
Acorn woodpecker (*Melanerpes formicivorous*)	Yes	Unknown	Female	Mumme et al. 1983
Smooth-billed ani (*Crotophaga ani*)	Yes	Unknown	Female	Loflin 1982
Groove-billed ani (*C. sulcirostris*)	Yes	Unknown	Female	Vehrencamp 1977
Noisy miner (*Manorina melanocephala*)	Colonial	Male	Male	Dow 1978, Whitmore 1986
Purple martin (*Progne subis*)	Yes	Unknown	Male	Brown and Bitterbaum 1980
Tree swallow (*Tachycetina bicolor*)	No	Unknown	Unknown	Shelley 1934
White-winged chough (*Cocorax melanocephalus*)	Yes	Unknown	Unknown	Heinsohn 1988
Mexican jay (*Aphelocoma ultramarina*)	Yes	Unknown	Unknown	Trail et al. 1981
Australian magpie (*Gymnorhina tibicens*)	Yes	Unknown	Unknown	Rowley 1973
Arabian babbler (*Turdoides squamiceps*)	Yes	Unknown	Unknown	Zahavi 1990
Starling (*Sturnus vulgaris*)	Yes	Female	Female	Feare 1984; L. Van Elsecker, personal communication

* Osprey are group living in some areas and solitary in others.

1987). In gulls, more chicks are killed than adopted (Pierotti and Murphy 1987), and all this killing is done by males. Male gulls attack all chicks that they observe entering their territories (Hunt and McLoon 1975; Hunt and Hunt 1976). Male gulls also attack the first chicks to fledge on a colony and attack all fledged young until their own chicks have fledged (Pierotti 1980; R. Pierotti, unpublished observations). These attacks rarely involve cannibalism since only a few gulls in any single colony are cannibals, and these eat only newly hatched chicks (Parsons 1971; Pierotti 1982*b;* Pierotti and Murphy 1987).

The highest rates of attacks on unrelated offspring have been observed to be directed at the offspring of near neighbors by male gulls that have lost their own offspring (Davis and Dunn 1976; Pierotti 1980, 1981, 1987). Such behavior has previously been described as "spiteful" (Davis and Dunn 1976; Pierotti 1980; Sherman 1981), but it may be more appropriate to interpret such infanticidal aggression as attempts to reduce the possibility of adoption by individuals that would be susceptible to accepting unrelated offspring and forced to pay a high physiological cost in caring for unrelated chicks.

Male seabirds do not abandon their breeding territories after losing offspring since breeding space is often a limited resource (Pierotti 1981), and birds that have lost their own offspring are physiologically primed for breeding with no offspring of their own to raise. Adoption is likely to occur under these circumstances and has been observed in gulls that have lost their own offspring or have not bred during the year they adopted (Graves and Whiten 1980; Pierotti 1980).

Incubating male black skimmers, *Rhynchops nigra,* have been observed to pick up chicks that approached them while they were incubating or brooding their own chicks, fly out over water, and drop the chick (J. Quinn, personal communication). Skimmer chicks are often found killed but uneaten on breeding colonies (Burger and Gochfeld 1989). Since male skimmers expend more time and energy in chick rearing than females (Burger 1981*b*), this infanticide could prevent the occurrence of potentially costly adoption. Terns, genus *Sterna,* also attack wandering chicks prior to the time when their own chicks become highly mobile, yet after this time they may feed unrelated chicks frequently (Nisbet 1989; R. Pierotti, unpublished observations). Common and thick-billed murres, *Uria aalge* and *Uria lomvia,* and black-legged kittiwakes, *Rissa tridactyla,* will attack chicks that approach them on ledges and have been observed to toss chicks off cliffs (R. Pierotti, unpublished observations). These species have also been observed to adopt unrelated chicks (Birkhead and Nettleship 1987; Pierotti and Murphy 1987).

In addition to these highly colonial species with semiprecocial offspring, other species that are loosely colonial (most of which have altricial offspring) show adoption and aggression directed at wandering offspring (table 3). These species typically attack newly fledged offspring that attempt to insert themselves into a nest where the young have not yet fledged or solicit food from breeding adults other than their parents. Adoption appears to be more frequent in species that are less colonial since parents of more colonial species show greater capabilities of offspring recognition (Beecher 1982; Bustamante and Hiraldo, in press). However, 29 of the 30 species of birds in table 3 are regularly colonial or group-living, which suggests that offspring recognition in colonial species may fail with some

regularity. In addition, the pattern is different compared with the overall percentage of group-living versus solitary nesting birds ($P < .01$ by χ^2 test).

In only 14 species of birds were both the sex providing more care and the primary infanticidal sex identified (table 3). In 13 of these cases, males were the killers of unrelated offspring, and in all cases the sex investing more heavily during the posthatching periods committed the infanticide ($P < .001$ that both sexes are equally likely to be infanticidal by χ^2 test). Also, all but two of the species of birds that show adoption and alleged resource-based or pathological infanticide produce multiple offspring.

The exceptions are the two species of murres, which, like elephant seals, breed in very dense aggregations where confusion of offspring is highly likely. Like the gulls, skimmers, and terns described above, male murres feed the young for a period of weeks until the young leave the nest. At this point, the male takes the offspring to sea for a period of months, during which the young learn to feed (Scott 1973; D. Varoujean, personal communication).

In noisy miners, males provide most of the nutrition to the nestlings and have been observed to kill nestlings that were not their offspring (Whitmore 1986). Female noisy miners, however, are nondiscriminating and accept eggs and feed fledglings that are unrelated to them (Dow 1978, and personal communication). Starlings, *Sturna vulgaris,* are the one species where females have been observed to be the infanticidal sex, and data exist on patterns of investment during chick rearing. Female starlings perform most brooding and provide most of the food to nestlings, and 90% of the adults accompanying juveniles in feeding parties are females (Feare 1984), so female investment exceeds that of males.

In addition to killing nestlings, egg removal has been observed in a number of species. Since this egg removal is directed solely at eggs during time periods when the infanticidal individual cannot have been a parent of the egg, this behavior is functionally equivalent to mammals killing neonates before they leave a nest chamber. In the acorn woodpecker, *Melanerpes formicivorus,* females toss out all eggs that are laid in the shared nest cavity, before they have laid their first egg (Mumme et al. 1983). This leads to the destruction of about 35% of all eggs laid in groups with more than one breeding female. Some of these eggs are eaten, but the individual removing the egg rarely eats it immediately after removal, which would be expected if cannibalism were the purpose of the removal. Similar egg removals have been observed in gray-breasted jays, *Aphelocoma ultramarina,* by adults unrelated to the eggs they removed (Trail et al. 1981).

Within-group egg destruction with no observed eating of eggs has been observed in noisy miners (see above), Arabian babblers, *Turdoides squamiceps,* groove- and smooth-billed anis, *Crotophaga sulcirostris* and *Crotophaga ani,* white-winged choughs, *Pyrrhocorax,* and Australian magpies, *Gynorhina tibicens* (Rowley 1973; Vehrencamp 1977; Loflin 1982; Heinsohn 1988; Zahavi 1990). In each case, the individual destroying the egg was a nonparental adult and by destroying the egg did not have to provide care to nonfilial offspring.

Starlings, *Sturnus vulgaris,* rarely breed cooperatively, but intraspecific nest parasitism is common in this species, and newly "fledged" offspring have been observed to insinuate themselves into nests of conspecifics that contained

younger offspring (L. Van Elsecker, personal communication). Egg tossing, infanticide, and attacks on newly fledged offspring have been observed in starlings. Female starlings perform most brooding and provide most food to nestlings, and 90% of the adults accompanying juveniles in feeding parties are females (Feare 1984). Starlings are the one species where females are known to be the infanticidal sex.

In contrast to birds with semiprecocial offspring, and the few species with altricial offspring that show evidence of both adoption and infanticide, adoption is common and infanticide is unreported from species of birds with precocial offspring (Savard 1987; Pierotti 1988). Swans, geese, ducks, shorebirds, grouse, and ratites have all been reported to adopt and guard young that join their brood (Pierotti 1988; Martin 1989). This tendency to adopt may result because adults with precocial young do not feed their offspring and there is no additional cost to guarding unrelated offspring that join the brood. In fact, since the major cause of juvenile mortality in precocial chicks is predation, there may even be a benefit to both parents and offspring of having additional offspring in the group either through increased awareness of predators or by diluting the effects of predation through a "selfish herd effect" (Hori 1964; Hamilton 1971; Gorman and Milne 1972; Pierotti 1988).

GENERAL DISCUSSION

It is likely that numerous examples of infanticide that have been interpreted as either pathological behavior or the result of possible competition for resources may instead be interpreted as the result of an intergenerational conflict between young seeking parental care from unrelated adults and adults attempting to prevent caring for unrelated young.

For example, the idea that such infanticide is the result of social pathology does not account for the widespread occurrence of such behavior or its apparent relationship with adoption. In the literature on free-living animals, no examples of pathological infanticide could be found from species that did not also show adoption. Also, many of the individuals reported to show such pathological behavior appeared to be completely normal in all other behaviors. In the future, evidence needs to be provided of general pathological behavior in infanticidal individuals, or specific evidence concerning the pathological nature of the infanticidal act should be provided if pathology is to be invoked as the cause of infanticide.

Similarly, evidence should be provided that resources in question are actually, or even potentially, limiting for resource competition to be invoked as an explanation for infanticide. Among mammals showing infanticide that is not satisfactorily accounted for under cannibalism, sexual selection, or parental manipulation, evidence of resource limitation has only been presented for Belding's ground squirrel (Sherman 1981), yet resource competition is routinely invoked as an explanation for infanticide.

Among birds showing infanticide and adoption, 16 of the 23 species feed either on marine fishes and invertebrates or on flying insects, neither of which is a

defendable or limited resource. Many of these species feed either in groups or cooperatively, so that there may be greater benefits than costs from increased numbers of conspecifics. This would reduce the likelihood of infanticide being caused by competition for limited resources. Finally, and most problematically for the resource competition hypothesis, no one has advanced an explanation for why species that suffer from competition for resources so intense that they are forced to kill neonates and nestlings should also show adoption of similar offspring under the same conditions that supposedly lead to infanticide.

I would be remiss in pointing out that the reciprocal case is also true. Prevention of adoption should not be invoked as an explanation for infanticide unless adoption, or a high frequency of wandering offspring, has been shown to exist in that species.

Species showing infanticide basically conform to my four major predictions. Nineteen of 21 species of mammals and 25 of 30 species of birds live in groups (table 2), where offspring have greatly increased opportunities to switch parents. In addition, all infanticide that does not involve filial killing, cannibalism, or sexual selection appears to be committed primarily or exclusively by the sex investing more heavily in postpartum (or posthatching) parental care. This suggests that individuals that would have to increase their workload (and their potential costs of reproduction, in the sense of Bell 1980) kill nonfilial offspring at a time when such offspring can clearly be recognized as such. Finally, all species that show adoption and infanticide have either multiple young per litter or brood (larids, skuas, raptors, swallows, carnivores, rodents, ungulates); live under conditions where offspring can be easily confused (elephant seals, murres); or live under social conditions where adults may be forced to accept unrelated offspring as a consequence of pairing (*Homo sapiens*).

It has been suggested that adoption occurs primarily between close genetic kin (Waltz 1981; Riedman 1982). With regard to this argument, it is worth noting that (*a*) infanticide is as common, if not more common, in most species where adoption has been observed to occur with regularity and (*b*) the same individual adults that will attack and kill juveniles which approach them or their breeding area, will often accept the same juvenile if it arrives unobserved or after they have lost their own offspring (Graves and Whiten 1980; Pierotti 1980; Riedman and LeBoeuf 1983; Pierotti and Murphy 1987; Pierotti et al. 1988; Nisbet 1989, and personal communication).

Given the above, kin selection is only likely to be important if it can be demonstrated that adults discriminate between kin and nonkin and adopt the former and kill the latter. Evidence on this point is equivocal. In *Mus* and *Lemmus,* colonies founded from several unrelated pairs showed infanticide, whereas populations started from a single pair showed no infanticide (Brown 1953; Semb-Johansson et al. 1979). In ground squirrels, infanticide was directed primarily at nonrelatives, but some sisters, aunts, and female cousins killed juveniles (Sherman 1981; Balfour 1983; Waterman 1984). In contrast, in prairie dogs and carnivores, infanticide is directed almost exclusively at relatives (MacDonald and Moehlman 1984; Hoogland 1985). In birds with semiprecocial offspring, aggression is directed at all wandering offspring, regardless of relatedness (Pierotti 1980; Pierotti et al.

1988; R. Pierotti, personal observation). Given this range of results, it is unlikely that kin selection provides a unitary explanation. An alternative explanation is that adults adjust their behavior to the likelihood of adoption.

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LITERATURE CITED

Arvola, A., M. Ilmen, and T. Koponen. 1962. On the aggressive behaviour of the Norwegian lemming (*Lemmus lemmus*) with special reference to the sounds produced. Archivum Societatis Zoologicae-Botanicae Fennicae 'Vanamo' 17:80–101.

Ayer, M. L., and J. M. Whitsett. 1980. Aggressive behaviour of female prairie deer mice in laboratory populations. Animal Behaviour 28:763–771.

Balfour, D. 1983. Infanticide in the Columbian ground squirrel, *Spermophilus columbianus*. Animal Behaviour 31:949–950.

Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. Evolution 24:546–559.

Beecher, M. D. 1982. Signature systems and kin recognition. American Zoologist 22:477–490.

Bell, G. 1980. Costs of reproduction. American Naturalist 116:45–76.

Bertram, B. C. R. 1975. Social factors influencing reproduction in wild lions. Journal of Zoology (London) 177:462–482.

Birkhead, T. R., and D. N. Nettleship. 1987. Alloparental care in the common murre. Canadian Journal of Zoology 65:1630–1637.

Boness, D. J. 1990. Fostering behavior in Hawaiian monk seals: is there a reproductive cost? Behavioral Ecology and Sociobiology 27:113–122.

Boonstra, R. 1980. Infanticide in microtines: importance in natural populations. Oecologia (Berlin) 46:262–265.

Brooks, R. J. 1984. Causes and consequences of infanticide in populations of rodents. Pages 331–348 *in* G. Hausfater and S. B. Hrdy, eds. Infanticide: comparative and evolutionary perspectives. Aldine, New York.

Brown, C. R., and E. J. Bitterbaum. 1980. Implications of juvenile harassment in purple martins. Wilson Bulletin 92:452–457.

Brown, R. Z. 1953. Social behavior, reproduction, and population changes in the house mouse. Ecological Monographs 23:217–240.

Burger, J. 1981*a*. On becoming independent in herring gulls: parent-young conflict. American Naturalist 117:444–456.

———. 1981*b*. Sexual differences in parental activities of black skimmers. American Naturalist 117:975–984.

Burger, J., and M. Gochfeld. 1989. The black skimmer. Columbia University Press, New York.

Bustamante, J., and F. Hiraldo. In press. Natural adoptions of fledglings in black and red kites. Animal Behaviour.

Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge.

Cox, M. R. 1892. Cinderella: 345 variants. Folklore Society, London.
Daly, M., and M. Wilson. 1984. A sociobiological analysis of infanticide in humans. Pages 487–502 *in* G. Hausfater and S. B. Hrdy, eds. Infanticide: comparative and evolutionary perspectives. Aldine, New York.
———. 1988. Evolutionary social psychology and family homicide. Science (Washington, D.C.) 242:519–524.
Davis, J. W. F., and E. K. Dunn. 1976. Intraspecific predation and colonial breeding in the lesser black-backed gull. Ibis 118:65–77.
Donazar, J. A., and O. Ceballos. In press. Attainment of food by fledgling Egyptian vultures (*Neophron percnopterus*) through nest-switching and acceptance by foster adults. Ibis.
Dow, D. D. 1978. Reproductive behavior of the noisy miner, a communally breeding honeyeater. Living Bird 16:163–185.
———. 1979. The influence of nests on the social behavior of males in *Manorina melanocephala*, a communally breeding honeyeater. Emu 79:71–83.
Drent, R. H. 1970. Functional aspects of incubation in the herring gull. Behaviour 17(suppl.):1–132.
Egoscue, H. J. 1957. The desert woodrat: a laboratory colony. Journal of Mammalogy 38:472–481.
Eisenberg, J. 1981. The mammalian radiations. University of California Press, Berkeley and Los Angeles.
Ellis, D. H., and D. L. Groat. 1982. A prairie falcon fledgling intrudes at a peregrine falcon eyrie and pirates prey. Raptor Research 16:89–91.
Elwood, R. W., and M. C. Ostermeyer. 1984. Infanticide by male and female Mongolian gerbils: ontogeny, causation, and function. Pages 367–386 *in* G. Hausfater and S. B. Hrdy, eds. Infanticide: comparative and evolutionary perspectives. Aldine, New York.
Errington, P. L. 1963. Muskrat populations. Iowa State University Press, Ames.
Feare, C. 1984. The starling. Oxford University Press, New York.
Festa-Bianchet, M., and D. A. Boag. 1982. Territoriality in adult female Columbian ground squirrels. Canadian Journal of Zoology 60:1060–1066.
Fetterolf, P. M. 1983. Infanticide and non-fatal attacks on chicks by ring-billed gulls. Animal Behaviour 31:1018–1028.
Fleming, A. S. 1979. Maternal nest defense in the desert woodrat. Behavioral and Neural Biology 26:41–63.
Fogden, S. C. L. 1971. Mother-young behaviour at grey seal breeding beaches. Journal of Zoology (London) 164:61–92.
Gonzalez, J. L., B. Heredia, L. M. Gonzalez, and J. C. Alonzo. 1986. Adoption of a juvenile by breeding Spanish imperial eagles during the postfledging period. Raptor Research 20:77–78.
Gorman, W. L., and H. Milne. 1972. Creche behaviour in the common eider. Ornis Scandinavica 3:21–25.
Graves, J. S., and A. Whiten. 1980. Adoption of strange chicks by herring gulls. Zeitschrift für Tierpsychologie 54:267–278.
Grossman, J. 1987. A prairie dog companion. Audubon 89:52–67.
Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295–311.
Hansen, R. M. 1957. Communal litters of *Peromyscus maniculatus*. Journal of Mammalogy 38:523.
Hausfater, G., and S. B. Hrdy. 1984. Infanticide: comparative and evolutionary perspectives. Aldine, New York.
Hayssen, V. D. 1984. Mammalian reproduction: constraints on the evolution of infanticide. Pages 105–124 *in* G. Hausfater and S. B. Hrdy, eds. Infanticide: comparative and evolutionary perspectives. Aldine, New York.
Heinsohn, R. G. 1988. Inter-group ovicide and nest destruction in cooperatively breeding white-winged choughs. Animal Behaviour 36:1856–1858.
Holley, A. J. F. 1984. Adoption, parent-chick recognition, and maladaptation in the herring gull. Zeitschrift für Tierpsychologie 69:9–14.
Hoogland, J. L. 1985. Infanticide in prairie dogs: lactating females kill offspring of close kin. Science (Washington, D.C.) 230:1037–1040.
Hori, J. 1964. The breeding biology of the shelduck. Ibis 106:333–360.
Hrdy, S. B. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethology and Sociobiology 1:13–40.

Hrdy, S. B., and G. Hausfater. 1984. Comparative and evolutionary perspectives on infanticide: introduction and overview. Pages xiii–xxxv *in* G. Hausfater and S. B. Hrdy, eds. Infanticide: comparative and evolutionary perspectives. Aldine, New York.

Huck, U. W. 1984. Infanticide and the evolution of pregnancy block in rodents. Pages 349–366 *in* G. Hausfater and S. B. Hrdy, eds. Infanticide: comparative and evolutionary perspectives. Aldine, New York.

Hunt, G. L., Jr., and M. W. Hunt. 1976. Gull chick survival: the significance of growth rates, timing of breeding, and territory size. Ecology 57:62–75.

Hunt, G. L., Jr., and S. McLoon. 1975. Activity of gull chicks in relation to feeding by their parents: their potential significance for density dependent mortality. Auk 92:523–527.

King, J. 1973. Energetics of reproduction in birds. Pages 78–107 *in* D. S. Franer, ed. Breeding biology of birds. National Academy of Sciences Press, Washington, D.C.

Kinsey, K. P. 1977. Agonistic behavior and social organization of Allegheny woodrats. Journal of Mammalogy 58:417–419.

Labov, J. B. 1980. Factors influencing infanticidal behavior in wild male house mice. Behavioral Ecology and Sociobiology 6:297–303.

Labov, J. B., U. W. Huck, R. W. Elwood, and R. J. Brooks. 1985. Current problems in the study of infanticidal behavior in rodents. Quarterly Review of Biology 60:1–20.

Lack, D. 1968. Ecological adaptations for breeding in birds. Chapman & Hall, London.

LeBoeuf, B. J., and K. T. Briggs. 1977. The costs of living in a seal harem. Mammalia 41:167–195.

Leffelaar, D., and R. J. Robertson. 1985. Nest usurpation and female competition for breeding opportunities by tree swallows. Wilson Bulletin 97:221–224.

Loflin, R. K. 1982. Egg-burying behavior and intraspecific brood parasitism in smooth-billed anis. Paper presented at the 99th annual meeting of the American Ornithological Union, Chicago, June 15–20.

MacDonald, D. W., and P. D. Moehlman. 1984. Cooperation, altruism, and restraint in the reproduction of wild carnivores. Perspectives in Ethology 7:433–467.

Mallory, F. F., and R. J. Brooks. 1980. Infanticide and pregnancy failure: reproductive strategies in the female collared lemming. Biology of Reproduction 22:192–196.

Martin, K. 1989. Pairing and adoption by replacement male willow ptarmigan: behaviour, costs, and consequences. Animal Behaviour 37:569–578.

McLeod, P. J. 1990. Infanticide by female wolves. Canadian Journal of Zoology 68:402–404.

Michener, G. R. 1982. Infanticide in ground squirrels. Animal Behaviour 30:936–938.

Mock, D. 1984. Infanticide, siblicide, and avian nestling mortality. Pages 3–30 *in* G. Hausfater and S. B. Hrdy, eds. Infanticide: comparative and evolutionary perspectives. Aldine, New York.

Mumme, R. L., W. D. Koenig, and F. A. Pitelka. 1983. Reproductive competition in the communal acorn woodpecker: sisters destroy each others' eggs. Nature (London) 306:583–584.

Nisbet, I. C. T. 1989. Characteristics and frequency of adoption by common terns. Paper presented at the annual meeting of the Colonial Waterbird Society, Key Largo, October 26–29.

Nowak, R. M., and J. L. Paradiso. 1983. Walker's mammals of the world. 4th ed. Johns Hopkins University Press, Baltimore.

Oftedahl, O. T. 1985. Pregnancy and lactation. Pages 215–238 *in* R. E. White, ed. Bioenergetics of wild herbivores. Pergamon, New York.

Parsons, J. 1971. Cannibalism in the herring gull. British Birds 64:528–537.

Pierotti, R. 1980. Spite and altruism in gulls. American Naturalist 115:290–300.

———. 1981. Male and female parental roles in the western gull under different environmental conditions. Auk 98:532–549.

———. 1982*a*. Spite, altruism, and semantics. American Naturalist 119:116–120.

———. 1982*b*. Habitat selection and its effect on reproductive output in the herring gull in Newfoundland. Ecology 63:854–868.

———. 1987. Behavioral consequences of habitat selection in the herring gull. Studies in Avian Biology 10:119–128.

———. 1988. Intergenerational conflicts in species of birds with precocial offspring. Proceedings International Ornithological Congress 19:1265–1274.

Pierotti, R., and E. C. Murphy. 1987. Intergenerational conflicts in gulls. Animal Behaviour 35:435–444.

Pierotti, R., D. Brunton, and E. C. Murphy. 1988. Parent-offspring and sibling-sibling recognition in gulls. Animal Behaviour 36:620–621.

Polis, G. A., C. A. Myers, and W. R. Hess. 1984. A survey of intraspecific predation within the class Mammalia. Mammal Review 14:187–198.

Poole, A. 1982. Breeding ospreys feed fledglings that are not their own. Auk 99:781–784.

Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pages 152–292 *in* R. A. Paynter, ed. Avian energetics. Publication of the Nuttall Ornithology Club 15.

Riedman, M. L. 1982. The evolution of alloparental care and adoption in mammals and birds. Quarterly Review of Biology 57:405–435.

———. 1990. The pinnipeds. University of California Press, Berkeley and Los Angeles.

Riedman, M. L., and B. J. LeBoeuf. 1983. Mother-pup separation and adoption in northern elephant seals. Behavioral Ecology and Sociobiology 11:203–215.

Rosenblatt, J. S. 1990. Landmarks in the physiological study of maternal behavior with special reference to the rat. Pages 40–60 *in* N. Krasegnor and R. S. Bridges, eds. Mammalian parenting. Oxford University Press, New York.

Rowley, I. 1973. The comparative ecology of Australian corvids. II. Social organization and behaviour. CSIRO Wildlife Research 18:25–65.

Savard, J.-P. L. 1987. Causes and functions of brood amalgamation in Barrow's goldeneyes and bufflehead. Canadian Journal of Zoology 65:1548–1553.

Scott, J. M. 1973. Ecology of four syntopic diving birds. Ph.D. diss. Oregon State University, Corvallis, Oreg.

Semb-Johansson, A., R. Wiger, and C. E. Engh. 1979. Dynamics of freely growing, confined populations of the Norwegian lemming. Oikos 33:246–260.

Shelley, L. O. 1934. Tree swallow tragedies. Bird-banding 5:134.

Sherman, P. W. 1981. Reproductive competition and infanticide in Belding's ground squirrels and other animals. Pages 311–331 *in* R. D. Alexander and D. W. Tinkle, eds. Natural selection and social behavior. Chiron, New York.

Stanback, M. T., and W. D. Koenig. In press. Extent of and constraints on cannibalism in birds. *In* M. Elgar and B. Crespi, eds. Cannibalism: a comparative review. Oxford University Press, Oxford.

Stirling, I. 1975. Adoptive suckling in pinnipeds. Journal of the Australian Mammal Society 1:389–391.

Teillaud, P., and R. Campan. 1987. Sucking behavior of the wild boar in enclosures: effects of adoption. Abstracts of the International Ethology Conference 20:171.

Trail, P. W., S. D. Strahl, and J. L. Brown. 1981. Infanticide in relation to individual and flock histories in a communally breeding bird, the Mexican jay. American Naturalist 118:72–82.

Trivers, R. L. 1974. Parent-offspring conflict. American Zoology 14:249–264.

Turner, D. C., and P. P. G. Bateson. 1988. The domestic cat: the biology of its behaviour. Cambridge University Press, Cambridge.

Van Lawick, H. 1973. Solo. Collins, London.

Vehrencamp, S. L. 1977. Relative fecundity and parental effort in communally nesting anis. Science (Washington, D.C.) 197:403–405.

vom Saal, F. S. 1984. Proximate and ultimate causes of infanticide and parental behavior in male house mice. Pages 401–424 *in* G. Hausfater and S. B. Hrdy, eds. Infanticide: comparative and evolutionary perspectives. Aldine, New York.

Waltz, E. C. 1981. "Reciprocal altruism" and "spite" in gulls: a comment. American Naturalist 118:588–592.

Waterman, J. M. 1984. Infanticide in the Columbian ground squirrel. Journal of Mammalogy 65: 137–138.

Whitmore, M. 1986. Infanticide of nestling noisy miners, communally breeding honeyeaters. Animal Behaviour 34:933–934.

Wilson, E. O. 1975. Sociobiology. Harvard University Press, Cambridge, Mass.

Zahavi, A. 1990. Arabian babblers: the quest for social status in a cooperative breeder. Pages 103–130 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.